Breeding and Selection for Salt Tolerance by the Incorporation of Wild Germplasm into a Domestic Tomato

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Abstract. Crosses were made between a salt tolerant wild tomato [Lycopersicon cheesmanii spp. minor (Hook) C. H. Mull.] and a domestic cultivar (L. esculentum Mill. cv. Walter). Selections were made from resulting progenies for salt tolerance at germination, seedling establishment, and the reproductive stage of their life cycle. The selected progenies were tested for survival and fruit production in salinized solution culture experiments, and in field greenhouse trials where they were irrigated with various dilutions of seawater applied to sand. Salt tolerance was shown to be a heritable trait. Plants selected from the F2 and successive backcrosses to ‘Walter’ survived and produced fruit when irrigated with up to 70% seawater in the sandy soil culture trials, whereas ‘Walter’ did not survive.

The ever increasing demand for agricultural products is now requiring a reassessment of the production potential of low-quality land and water resources (12, 14, 21). We are rapidly approaching an era in which it will be necessary to breed economically useful plants that are adapted to lower-grade inputs and higher environmental stresses than are most present-day cultivars (14, 15, 20, 36). Specifically, improved efficiency of mineral nutrient and water use, and increased tolerance of saline and other poor quality water will be of importance (14, 17). Phenomenal improvements in yield, quality, and other desirable traits of crops have been achieved by plant breeders (18, 30). Most of that work, however, was done under conditions of optimal inputs of water and mineral nutrients. As a result there may have been inadvertent selection of genotypes that are relatively inefficient in the use of water and nutrients when their supplies are less than optimal (8, 26). In addition, little has been done to adapt crops by genetic means to other unfavorable conditions in the mineral environment (soil and water). Adaptation of crops to saline situations is among these neglected areas of potentially useful research and development (14). Although differences in salinity tolerance among genera are recognized (3, 10, 19, 28, 31, 32), few investigations have dealt with interspecific and intraspecific diversity in respect to salt tolerance (11, 24, 25, 27, 29). The genetics and physiology of salinity tolerance are only now being given the attention they deserve and the chances for crop improvement seem bright (11, 13, 14, 24, 27). The primary objective of the work reported here was to examine the hypothesis that salt tolerance can be genetically transferred from a wild, economically useless tomato species to a domestic salt sensitive variety.

Experiments were carried out in 4 consecutive growing seasons, 1976–1979. Dilutions of seawater were used to salinize the growth medium. Sea salts were chosen because the complement of ions is similar in complexity to that of many highly saline soil solutions, which often contain excessive amounts of potentially detrimental constituents such as boron, magnesium, sulfate, and carbonate, in addition to sodium chloride. The use of seawater has the added benefit of having a direct bearing on areas plagued by saltwater encroachment into groundwater supplies near deltas and coastal estuaries. An ultimate possibility would be the development of crops capable of using the nutrients and water contained in the oceans for production of food and other biomass along the edges of the extensive coastal deserts of the world.

Materials and Methods

The crossing and selection program was initiated using a wild, salt tolerant tomato, Lycopersicon cheesmanii spp. minor (28, 29), as the pollen parent and a fresh market greenhouse cultivar, L. esculentum cv. Walter. These experiments were carried out in greenhouses at the University of California at Davis under ambient light and day and night temperatures of 28 ± 2°C and 20 ± 2°C, respectively. The F2 generation from this cross was screened for salt tolerance at germination and the seedling stage using 2 selection methods.

Several hundred hybrid seeds were planted on stainless steel screens covered with boiled cheesecloth. These were placed on rectangular 12-liter containers of aerated, half-concentration modified Hoagland solution (10, p. 39) at such a height that the solutions were in contact with the screen seed bed. A full stand of 7–8 cm tall seedlings developed in about 14 days. The nutrient solutions were renewed and then progressively salinized with either NaCl or a synthetic sea salt mix (Rila Marine Mix, Rila Products, P. O. Box 114 Teaneck NJ 07666). Salts were added at concentrations equivalent to 10% seawater at 4–5 day intervals. The final salt concentration was equivalent to 60% seawater (EC 28–30 mmhos/cm) or about 300 mM NaCl. Solution pH was kept between 5.5–7.0.

The cultures were maintained until only a few presumably salt tolerant seedlings remained alive. These were removed from the screens and each was inserted into the central hole of a cork stopper where it was held in place by Dacron batting. The corks were then placed in opaque lids of containers of salinized nutrient solution. The salinity of these solutions was progressively reduced.
from the equivalent of 60% seawater down to half concentration modified Hoagland solution in 3 successive steps at 4-5 days intervals. Those plants surviving the step-down procedure were planted in 3-liter pots of sand-peat soil (3:1) and maintained for evaluation of salt tolerance at later stages of their life cycle.

The other method used to evaluate resistance to salt at early stages of development followed similar planting procedures except that the nutrient solutions were salted from the beginning of the germination period. Selection pressure was maintained at 40-50% seawater salinity. The containers were covered with clear plastic wrap to minimize evaporation and contamination during the relatively long (up to 5 weeks) period of germination and seedling establishment. Those plants that germinated and grew to 6-8 cm in height were transferred, the solution salinity was stepped down and the seedlings were maintained as outlined earlier. For selections of plants ultimately superior in salt tolerance throughout their life cycle the second procedure proved to be superior and was used for all selections after the 1977 trials.

Consecutive backcrosses were made using ‘Walter’ as the recurrent seed parent. Plants of the F1 and F4 generations from the original crosses and several F2, 5 of backcrosses were also stress selected.

Evaluation of salt tolerance after seedling establishment was carried out in greenhouse shelters on stabilized sand dunes at the University of California Bodega Marine Laboratory. The Bodega experiments ran from April through October for 4 consecutive years (1976-1979).

The trials were in two 3 \times 12 m plastic-covered shelters, each divided into 2 plots. Both were equipped with exhaust fans, air circulators, and a heater.

All plantings were on raised beds in soil classified as loamy sand. All plots were leached between seasons and tested between plantings to assure that no salt was carried over from the previous year’s experiments. The various salt treatments were randomly assigned to the plots each year.

The previously selected uniform plants, 20-25 cm in both height and canopy diameter, were spaced 3 to 5 plants per 3 m bed with 5 or 6 beds per plot. Plantings followed a randomized location assignment that included both parents and selected progeny. Density ranged from 15 to 25 plants per plot depending on the salinity of the irrigation water to be used, the higher salt treatments having the highest planting density.

The plant material tested included the 2 parents, F1, F2, and F4 progeny of the cross between L. cheesmanii and ‘Walter’, backcrosses 1 and 2 (to ‘Walter’) and F3, 5 of the backcrosses, all of which were salt-stress selected during each generation. The total numbers of plants evaluated were 96, 70, 75 and 84, for the years 1976-1979, respectively.

All plots were fertilized with 50 g of 14N-6P-12K slow release fertilizer and 12 g of single superphosphate per plant placed below and to one side of the root mass at the time of transplanting. After 3 to 4 weeks the plants were tied to redwood stakes and pruned weekly to maintain a single primary stem.

Irrigation was with various dilutions of seawater and a fresh water control. Concentrations of 30, 50 and 70% seawater were used. Application rate was 1500 liters per plot added at 4 to 7 day intervals. Water was channeled into the houses and distributed to the furrows on both sides of the bed in polyethylene tubing, with flow gates to insure uniform distribution within each plot. Each irrigation brought the water level to the tops of the beds.

Precautions were taken to insure that no root system was established outside the perimeter of the plastic shelters. Each plot was surrounded with a continuous high-impact polystyrene root barrier buried to a depth of 80 cm and located inside the base of the shelter walls.

All plots were given irrigations with fresh water after transplanting to reduce transplant shock and hasten root development. A progressive salinization scheme was then employed in the salt plots starting 10 days after transplanting in each year’s experiment. All salt water treatments received 2 irrigations with 30% seawater. The 50 and 70% plots then received 2 irrigations with 50% seawater. Finally, the 70% plots were switched to 70% seawater for the duration of the experiments.

All flowers and fruits were removed from the plants of all treatments during the progressive salinization irrigations. The harvest period for all experiments was from June to October. Fruit was picked at the red ripe stage once a week, counted, sized, and weighed on a per plant basis. Dissolved solids (fruit) were measured periodically using a refractometer (Brix index). All fruit was removed at the end of each experiment and the immature green tomatoes assigned an average size and weight based on the individual plant means of all the previous fruit harvests for each treatment in that season. It was assumed that the immature fruit would eventually have been similar to the average for all the previous harvests for each plant. These assigned last-harvest data were only a small percentage of the season’s total production. Comparisons were made (analysis of variance) among the data for each selection at the different salinities including the fresh water controls, and among those of different selections at a given salinity. A qualitative evaluation of factors such as vigor and response to salinity was used to rate the various plants in each treatment. Symptoms of salt stress included stunting, darkening of leaf color, marginal chlorosis and necrosis, an increase in the number of flowers produced, and a decrease in mature fruit size. All of these became more pronounced with increasing salinity.

The environmental parameters monitored, included irrigation water quality (salinity and pH), soil solution salt concentration and pH, shelter temperature and relative humidity, and insect infestation. Soil samples were taken from 5, 30 and 50 cm depths at the beginning, middle and end of the experiments. Soil moisture data and saturation paste extracts were used to make conductivity and pH measurements. Water quality parameters were maintained close to the desired salt concentrations of 30, 50, and 70% seawater (Table 1). Average daytime temperatures ranged from 30–40°C and occasionally reached the mid 40s. Maximum temperatures were often in excess of what is generally considered ideal for tomato culture and contributed to the overall stress being applied to the salt treatments. Night temperatures averaged 14–17°C, occasionally down to 9–10°C because of heater failure or cold weather. The daytime relative humidity range was 20–45% and at night 80–100%. The salt concentration of the soil solution was generally 1.5 to 2.5 times as high as that of the irrigation water applied except for the controls in which soil solution EC ranged from 3 to 5 mmhos/cm.

Table 1. Quality of water used to irrigate tomato selections being evaluated for salt tolerance.

<table>
<thead>
<tr>
<th>Year</th>
<th>Fresh water EC</th>
<th>30% SW</th>
<th>50% SW</th>
<th>70% SW</th>
<th>100% SW</th>
<th>EC</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>1.20</td>
<td>7.6</td>
<td>17.3</td>
<td>7.4</td>
<td>25.8</td>
<td>7.4</td>
<td>33.1</td>
</tr>
<tr>
<td>1978</td>
<td>0.46</td>
<td>7.6</td>
<td>17.2</td>
<td>7.6</td>
<td>22.2</td>
<td>7.5</td>
<td>34.1</td>
</tr>
<tr>
<td>1979</td>
<td>0.48</td>
<td>7.7</td>
<td>16.8</td>
<td>7.6</td>
<td>25.0</td>
<td>7.5</td>
<td>34.3</td>
</tr>
<tr>
<td>Expected</td>
<td></td>
<td>15.7</td>
<td></td>
<td>25.0</td>
<td>33.5</td>
<td>45.9</td>
<td></td>
</tr>
</tbody>
</table>

2Data based on the mean of samples taken from each irrigation during the experiments at Bodega Bay.

3SW denotes seawater.

Insect pest problems were minor, white flies being the most bothersome. Effective control was maintained by an occasional foliar application of synthetic pyrethroids.

Results

Breeding and selection: general observations. The post-emergence progressive salination and step-down technique (first method) produced a small number (less than 2% of the total seeds planted) of potentially salt tolerant selections for later transplant to the Bodega field site. The second method of selection using a salinized germination medium was even more severe. In the initial selections, less than 1% of the seeds germinated and established viable plants during continuous exposure to saline solutions equivalent to 40–50% seawater. The germination rate improved with each successive backcross. As more uniform germplasm was developed, seedling establishment approached 50% in the BC₃ generation when 50% seawater was used as the selection medium.

Survival data from the first 2 Bodega field experiments suggested that continuous exposure to salt was a better indicator of salinity tolerance than the progressive salination technique. The constant exposure method was used in all subsequent selections. Those plants stress-selected with NaCl rather than sea salt were less successful in survival and fruit production when exposed to diluted seawater at the Bodega site. Seawater salt was therefore used in the medium for all subsequent selection studies.

Seedlings of the domestic ‘Walter’ could not be established at the stress levels used to select the tolerant individuals in the segregating progenies. The salt tolerance of the L. cheesmanii ecotype had previously been established (29).

The phenotypic characteristics of the selected F₂ plants were intermediate between those of the 2 parents. The F₂ selections retained a bushy indeterminate growth habit with light green, highly pubescent leaves and stems. The fruit was produced on cymes similar to those of the wild parent and was orange in color but larger — 2 to 3 cm in diameter compared with 1 cm for the L. cheesmanii fruit. The F₃ and F₄ generations were also salt-stress selected and the influence of the tolerant parent was apparent in terms of salt tolerance, growth habit, and fruit size.

The selected plants of the BC₁ were more like the ‘Walter’ parent in appearance, and the fruit size was about twice that of the F₂ plants. Mature fruit color ranged from red to orange with a mean fruit diameter of about 3.7 cm when grown in fresh water. The BC₁ generation retained a substantial level of salt tolerance in terms of both survival and yield under saline conditions.

The selected BC₂ plants were intermediate in appearance between ‘Walter’ and the first backcross, with a mean fruit diameter of about 4.5 cm. A high degree of salt tolerance was maintained. Reduction in fruit size under saline conditions was slight (Fig. 1).

The selected progeny from self-pollinated BC₁ and F₃BC₁ (‘Walter’ x F₃) plants were similar to the selected BC₂ in habit but were more vigorous in growth and fruit production. Fruit size and color were similar to those of the first backcross.

Bodega Bay trials, 1976 planting. The first season’s experiments were devoted largely to the development of cultural techniques and to the evaluation of the overall feasibility of irrigation with highly saline water. In all salinity treatments the selected progeny were superior to the domestic cultivar and similar to the wild parent in their ability to tolerate salt.

Accumulated yield data were not prepared for this trial because of inconsistencies in cultural techniques used to maintain the various entries and treatments. Such data are presented for the results of the subsequent experiments.

1977–1979 plantings. The wild L. cheesmanii species (pollen parent) was planted in all treatments for each year’s experiments. It survived, flowered, and produced fruit in all trials but no yield data were taken (see discussion). Representatives from all of the selected progeny tolerated higher salinity levels than the ‘Walter’ which did not survive the 70% seawater treatment (Table 2). Progeny included the F₂, F₃, and F₄, BC₁ and BC₂ generations and several selected intermediates.

Fruit size and number were influenced by salinity in nearly all plants tested. Fruit of ‘Walter’ was most severely diminished in both size and number when compared with that of the fresh water controls, while fruit of the successive crosses was less affected by the salt stress conditions. The numbers of fruit produced by the selections remained high in all salt treatments when compared with those of ‘Walter’ (Table 3). The exceptions were the initial F₂ selections which were quite small in terms of both fruit number and size in all treatments. Fruit of subsequent F₂ and F₃ selections improved substantially in number while their size remained similar to that of the F₂. Fruit size increased with each successive backcross and was less adversely affected by the various salt treatments (Fig. 1). The 50% seawater treatment reduced the size of ‘Walter’ fruit to 12% (volume) and the number produced to 43% of that of the controls. In comparison, the BC₂ selections were reduced to 22% in size but the number of fruit produced per plant was 119% that of the controls (Fig. 2, Table 3). All of the surviving progenies flowered continuously and set fruit at 70% seawater. Fruit number remained high in the successive backcrosses even as size increased.

Table 2. Plant survival expressed as percent of total planted at various salt levels.

<table>
<thead>
<tr>
<th>Irrigation water</th>
<th>Walter</th>
<th>F₂</th>
<th>BC₁</th>
<th>BC₂</th>
<th>F₃BC₁</th>
<th>1401</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fresh water</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>50% SW²</td>
<td>92</td>
<td>100</td>
<td>100</td>
<td>75</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>50% SW</td>
<td>46</td>
<td>83</td>
<td>78</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>70% SW</td>
<td>0</td>
<td>67</td>
<td>45</td>
<td>40</td>
<td>67</td>
<td>80</td>
</tr>
</tbody>
</table>

²SW denotes seawater.
to the selections under both stress and nonstress conditions. Salt incorporated into the selections, which exhibited higher solids selection and the Walter parent. Stress tended to magnify the differences in flavor between the plants exposed to salt stress. It appeared to be a function of both several of the salt treatments (Table 5). The flavor components were markedly increased and imparted a very intense tomato taste produced no fruit at the highest salt treatment. The per plant yield of the F2 selections was low initially but yields increased substantially in successive generations and backcrosses.

The dissolved solids content of the fruit increased in all the plants exposed to salt stress. It appeared to be a function of both the salinity of the irrigation water and of the wild germplasm incorporated into the selections, which exhibited higher solids levels than did ‘Walter’ in the fresh water controls as well as in several of the salt treatments (Table 5). The flavor components were markedly increased and imparted a very intense tomato taste to the selections under both stress and nonstress conditions. Salt stress tended to magnify the differences in flavor between the selections and the Walter parent.

**Discussion**

Improvement in the salt tolerance of tomatoes was suggested as early as 1941 by Lyon (22) in a paper on responses of the tomato to sodium sulfate. Dewey (4) and Epstein (9, 10) have discussed selection and breeding for salt tolerance in general terms. For a brief account of the development of the concept of a genetic approach to salt problems see Epstein et al. (14). The strategy used in the present project, of imparting a desirable trait to a domestic crop from a wild relative possessing it, has been discussed by Harlan (18). It does not so far seem to have been used in the development of salt-tolerant crops.

Several researchers have evaluated various aspects of salt relations in the tomato. These studies included species and cultivar evaluations (3, 5, 7, 25, 32), the role of Na as a nutrient under salt stress (6, 23), Na and K interactions under low or high salt conditions (1, 7, 16, 23), and the development of management techniques to optimize yields under various saline conditions (2, 33, 34, 35). Selection and breeding for tolerance of high salt levels follow as a logical step.

In evaluating the data, several trends become apparent. Salt tolerance was retained in the germplasm as demonstrated by the survival of the successive backcrosses in the 70% seawater treatment, which was always fatal to ‘Walter.’ Improved germination percentages in successive selections of progeny of the original cross at a given salt stress indicated that the selections became more uniform in their tolerance of salt at germination and seedling establishment with each successive backcross.

There is some evidence that the yield potential of the selections is higher than is reflected in the data in Tables 3 and 4. Substantial pruning was necessary to manage the plants, which were naturally rank and bushy when compared with ‘Walter’.

No yield data were taken for the L. cheesmanii parent because of its small fruit size, and because it flowered and fruited predominantly during periods of day length similar to those of its natural equatorial environment. This occurred only at the beginning and end (early spring and late fall) of the season at Bodega. This trait was not expressed in any of the selected crosses.

**Table 3. Average fruit production of the domestic cultivar ‘Walter’ and selections of progenies from crosses made with the wild L. cheesmanii.**

<table>
<thead>
<tr>
<th>Irrigation water</th>
<th>‘Walter’</th>
<th>F2</th>
<th>BC1</th>
<th>BC2</th>
<th>F3BC1</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Freshwater</td>
<td>53</td>
<td>54</td>
<td>141</td>
<td>58</td>
<td>258</td>
<td>80</td>
</tr>
<tr>
<td>30% SW</td>
<td>43</td>
<td>49</td>
<td>167</td>
<td>73</td>
<td>183</td>
<td>50</td>
</tr>
<tr>
<td>50% SW</td>
<td>23</td>
<td>64</td>
<td>78</td>
<td>81</td>
<td>135</td>
<td>36</td>
</tr>
<tr>
<td>70% SW</td>
<td>0</td>
<td>31</td>
<td>62</td>
<td>57</td>
<td>68</td>
<td>14</td>
</tr>
</tbody>
</table>

2Standard error derived from analysis of variance for the parents and generations in each treatment. SW denotes seawater.

**Table 4. Average fruit yield on a per plant basis, given in grams fresh weight and as a percentage of the fresh water controls for cv. Walter and selections of progenies from crosses made with the wild L. cheesmanii.**

<table>
<thead>
<tr>
<th>Irrigation water</th>
<th>Walter</th>
<th>F2</th>
<th>BC1</th>
<th>BC2</th>
<th>F3BC1</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Freshwater</td>
<td>7436</td>
<td>100</td>
<td>441</td>
<td>100</td>
<td>3772</td>
<td>100</td>
</tr>
<tr>
<td>30% SW</td>
<td>2343</td>
<td>32</td>
<td>286</td>
<td>65</td>
<td>1993</td>
<td>53</td>
</tr>
<tr>
<td>50% SW</td>
<td>690</td>
<td>9</td>
<td>316</td>
<td>72</td>
<td>348</td>
<td>9</td>
</tr>
<tr>
<td>70% SW</td>
<td>0</td>
<td>0</td>
<td>108</td>
<td>24</td>
<td>163</td>
<td>4</td>
</tr>
</tbody>
</table>

2SE derived from analysis of variance for the parents and generations in each treatment. SW denotes seawater.

**Fig. 2. Relative change in fruit size (volume), comparing several entries at various salinities with their fresh water controls.**
A potentially valuable trait incorporated in the selections from the wild parent was a high fruit solids content. This was evident under fresh water conditions as well as in several of the progeny grown under salt stress (Table 5). This rise in dissolved solids content was accompanied by an intense tomato flavor which increased with the level of salt applied. Taste tests suggested that high concentrations of sugars and acids were responsible for much of the intense flavor. This trait could lend itself to the improvement of fresh market tomatoes, while the implications of substantial increases in dissolved solids are obvious for the growers and processors of canning tomatoes. Similar increases in dissolved solids induced by salinity have been found by others (32).

The environmental parameters, specifically temperature and soil type, were factors that must be considered in the evaluation of the results. Temperatures were often high enough to produce significant stress in all treatments, resulting in pollen desiccation, flower abortion, and reduced growth rate which ultimately affected yields, especially in the salt treatments. The heat superimposed on the salt substantially increased the total physiological stress. Inasmuch as both salt and heat stress require physiological adaptations in the water economy of plants, the imposition of heat stress along with salinity may have been beneficial in the screening.

These experiments demonstrate a genetic component of salt tolerance that can be transferred through selection and breeding, and that improved tolerance of salinity is biologically feasible. While these selections lack some of the desirable traits of domestic cultivars, they provide evidence that substantially improved performance under the stresses of saline environments can be achieved. It is hoped that the germplasm now at hand can be used for the development of salt tolerant cultivars. Finally, related genotypes differing in salt tolerance, like those developed in this investigation, offer the opportunity for research on the mechanisms of salt tolerance and its genetic control.

### Literature Cited

Influences of Potassium, Cultivar, and Season on Tomato Graywall and Blotchy Ripening

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Abstract. ‘Healani’, ‘Homestead-24’, ‘Walter’, and ‘Flora-Dade’ tomatoes (Lycopersicon esculentum Mill.) were grown with 0, 93, 186, 372, or 744 kg K/ha during spring and fall to determine the influence of K rate, cultivar, and season on the separate fruit disorders of graywall (GW) and blotchy ripening (BR). Susceptibility to GW was determined by inoculating a GW-inducing type of bacteria, Erwinia herbicola (Dye), into the outer pericarp of immature green fruit. All 4 cultivars developed more GW without added K than with it during the spring season. In both field and greenhouse conditions, ‘Flora-Dade’ and ‘Homestead-24’ were more resistant to GW than ‘Healani’ and ‘Walter’. Natural GW, contrasted to bacterially induced GW, occurred in ‘Healani’ and ‘Homestead-24’ fruit grown with low K concentrations in a sand culture experiment. Both cultivars were free of natural GW with the high-K treatment. ‘Flora-Dade’ was resistant to natural GW under all K treatments. Fruit from all cultivars had significantly less BR with K fertilization in both seasons. Externally blotchy ripening (EBR) and internal blotchy ripening (IBR) were more severe in the spring than in the fall. ‘Healani’ showed resistance to yellow shoulder, the primary EBR symptom, which was severe during the spring in all other cultivars. ‘Healani’ was generally the most BR-resistant cultivar and ‘Flora-Dade’ the most BR-susceptible. Pericarp K concentration increased with K rate in all cultivars during both seasons, but differences in susceptibility to BR between cultivars were not associated with differences in pericarp K, Ca, Mg, or P content.

Graywall is a disorder of tomato fruits that occurs during maturation and ripening. Symptoms are grayish-brown discolorations seen through the outer fruit wall that may appear on small, immature green fruit as well as on ripe fruit. These areas may become slightly depressed and roughened. Internally, severe browning usually appears in the outer pericarp, especially in regions associated with the vascular bundles. GW is a disorder distinct from blotchy ripening. Hobson et al. (9) provide colored illustrations of both disorders.

Vascular browning was first described by Conover (4). Stoner (20) used the term GW to describe a disorder identical to Conover’s vascular browning. Cool night temperatures, shade, mist, and to some extent soil compaction all contributed to its occurrence (5). Affected fruits were usually found on vigorous plants beneath the foliage where they were shaded. GW was frequently found after periods of wet and cloudy weather.

Earlier workers tried to associate “internal browning” (probably GW) with tobacco mosaic virus (TMV) infection (2, 15). Others suggested that internal browning resulted from restricted movement of sugars into the developing fruit (13).

The most recent hypothesis of the cause of GW involves a pathogenic bacterial association in the fruit. Hall and Stall (6) isolated a pure culture of bacterium from ooze in the stem scar of chilled GW-affected fruit. Injection of the bacterium into the outer pericarp of green fruits before or after chilling at 3°C induced GW-like symptoms. Stall and Hall (18) reproduced GW symptoms by injecting crude extracts from GW-affected tissue into healthy fruits, while removing or killing the bacteria resulted in no GW development. Graywall was not specific to 1 type of bacteria (19), but an association was established between concentration of bacteria inside the fruit and visible browning. Stall et al. (17) could not attribute GW incidence to the presence of TMV, but proposed that both bacteria and TMV may be predisposing factors and not the primary cause of GW.

Increasing soil K reduced internal browning in TMV-inoculated plants (15). Hayslip and Iley (7) studied a combination of GW and BR symptoms of fruit and found that low-K treatments (high N/K2O ratios) resulted in more diseased fruits than high-K treatments (low N/K2O ratios). However, the influence of K on the separate disorders was not noted.

Blotchy ripening is another severe and economically important disorder affecting tomato fruit and appears externally as areas of yellow or orange discoloration intermixed with normal red areas. The discoloration may be random throughout the fruit surface or confined primarily to the shoulder region. “Yellow shoulder,” a form of BR that is distinct from sunburn, may be severe during certain years and seasons in red-ripe, Florida-grown tomatoes. A whitish discoloration of the pericarp and placenta tissue appears internally. In severe cases, brown lignified vascular strands are found in the outer pericarp. An extensive histological study of the